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Movement between habitats by unequal competitors: effects of finite population size on ideal free distributions

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ABSTRACT

Ecologists have frequently commented on the ability of Fretwell and Lucas' (1970) ideal free distribution (IFD) theory to approximate observed animal distributions, despite frequent violations of the assumption that competitors are of equal competitive ability. In a previous paper (Hugie and Grand, 1998), we provided an explanation for this phenomenon by recognizing that animals will often move between habitats for reasons other than simply to maximize resource payoffs, given perfect information about current payoffs in all habitats. When such 'non-IFD' movements are incorporated into an unequal competitors IFD model, the equilibrium distribution is predicted to resemble an IFD for equal competitors. Recently, this explanation was criticized based on the results of an individual-based simulation model (Ruxton and Humphries, 1999). Here, we show that this criticism is the result of assumptions that not only differ fundamentally from those of our original model, but also are unlikely to be met in nature. We also construct our own simulation model and apply it to both an infinitely large population scenario, as assumed by our original analytical model, and a finite population scenario in the form of an individual-based model. In doing so, we confirm the validity of our original results and extend our theory to finite populations.

Keywords: habitat selection, ideal free distribution, individual-based modelling, patch switching, population size, unequal competitors.

INTRODUCTION

Ideal free distribution (IFD) theory was developed to predict the distribution of animals across habitats differing in resource availability (Fretwell and Lucas, 1970; Fretwell, 1972). If all members of the population are equal in their ability to capture and consume resources, a single equilibrium distribution is predicted. This distribution is characterized by 'input-matching' of competitor numbers; that is, the ratio of the number of individuals between any two habitats will equal the ratio of the resource availabilities in those habitats. If, however, individuals within a population differ in competitive ability, a number of

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possible equilibria are predicted (Sutherland and Parker, 1985; Parker and Sutherland, 1986). All such distributions have the characteristic that the ratio of the sum of competitive 'units' between any two habitats equals the ratio of the resource availabilities in those habitats (i.e. 'input-matching' of competitive units, where competitive 'units' measure the relative ability of an individual to compete for resources). One of these distributions resembles an IFD for equal competitors in that total competitor numbers, as well as competitive units, 'match' the distribution of resources (Sutherland and Parker, 1985; Milinski and Parker, 1991). This resemblance between the predictions of the equal and unequal competitors IFD models has been used to reconcile the frequent observation that the distribution of experimental animals often approximates an equal competitors IFD despite measurable differences between individuals in competitive ability (Milinski and Parker, 1991). However, given that the unequal competitors model predicts a number of possible equilibria, it is unclear why this particular distribution would be observed more commonly than any other. Explaining this phenomenon is important because it could provide a justification for ignoring the complications introduced by competitive inequalities when predicting animal distributions in nature.

Hugie and Grand (1998) provided a novel explanation by recognizing that animals do not live in an 'ideal' world, moving between habitats simply to maximize resource payoffs given perfect information about the current payoff in each habitat. Instead, they distinguished between such 'IFD' movements and occasional movements between habitats that occur for a variety of 'non-IFD' reasons, including avoiding agonistic encounters, fleeing from predators and searching for mates. Although IFD movements will end once an ideal free distribution is reached, non-IFD movements can continue indefinitely (see Hugie and Grand, 1998). Hugie and Grand demonstrated that, when non-IFD movements are incorporated into an IFD model for unequal competitors, a single, stable distribution of competitors is predicted. Moreover, this equilibrium will often resemble the IFD for equal competitors in that total competitor numbers will come close to matching the distribution of resources.

Recently, Ruxton and Humphries (1999) questioned these conclusions. Ruxton and Humphries base their criticisms on the results of an individual-based model and their assertion that Hugie and Grand incorrectly interpreted the meaning of asymptotic stability in their analytic model. According to Ruxton and Humphries, when unequal competitors move for both IFD and non-IFD reasons, they will end up being distributed in any one of a set of possible distributions, just as in the original unequal competitors model.

One obvious difference between the models presented by Hugie and Grand (1998) and Ruxton and Humphries (1999) concerns the size of the competitor population. Hugie and Grand assumed a population sufficiently large that the stochastic nature of individual movements could be safely ignored. This assumption allowed them to solve their model analytically. In contrast, Ruxton and Humphries simulated the movements of a small number of competitors using an individual-based model. Ruxton and Humphries claim that, apart from this difference, the assumptions of their model are identical to those of Hugie and Grand. This raises the question of whether the difference in the results of these two models is simply due to the difference in the population size they assume. Regardless, theoretical investigations into the effects of population size are necessary to determine whether the theory of Hugie and Grand can be generalized to finite (and small) populations. Here, we present a general model of competitor movements for IFD and non-IFD reasons, which mirrors the assumptions of Hugie and Grand (1998), and apply this model

to both large and finite population scenarios. In the latter case, we employ an individual-based approach, allowing our results to be compared directly with those of Ruxton and Humphries (1999).

As we shall show, the new model supports our earlier conclusions. Moreover, we shall demonstrate that these conclusions also apply to finite populations of ecologically relevant sizes. As stated previously (Hugie and Grand, 1998), when population size is large enough that the stochastic nature of individual movements can be safely ignored, the resulting competitor distribution will always converge on a single, stable distribution. When population size is finite, however, the stochastic nature of non-IFD movements will cause the distribution of competitors to vary over time: the smaller the population, the greater the observed variation. However, except for extremely small populations, such as those typical of aquarium studies, the competitor distribution will continue to resemble an equal competitors IFD, despite the presence of temporal variation. More importantly, even in these tiny populations, the *average* competitor distribution will resemble an equal competitors IFD. We conclude that the theory presented by Hugie and Grand (1998) is quite general and that non-IFD movements probably play an important role in determining the ecological distribution of competitors. Our investigations also reveal that the results of Ruxton and Humphries (1999) are due to unique assumptions that not only differ fundamentally from those of Hugie and Grand (1998), but also are unlikely to be met in nature.

We begin with simple verbal descriptions of our earlier analytic model and the large- and finite-population versions of the current numerical model. (The mathematical details of the model are presented in the Appendix. In addition, an interactive computer demonstration of the model is available* for the Microsoft Windows® operating system.) We then present the results of our current investigation. Finally, we outline and respond to Ruxton and Humphries' criticisms of our earlier paper.

HUGIE AND GRAND (1998) REVISITED

Hugie and Grand (1998) modelled the distribution of two competitor types differing in their ability to compete for resources (i.e. 'good' competitors and 'poor' competitors) across two habitats differing in resource availability (a 'good' habitat and a 'poor' habitat). Following Parker and Sutherland (1986), we assumed that resources were non-depleting and that competitive abilities remained constant across habitats. We considered the dynamics of competitor movement between habitats for both IFD and non-IFD reasons and determined characteristics of the equilibrium that was reached. Although the model was written in general terms, for the purpose of this simplified explanation [and to allow for direct comparisons with both Ruxton and Humphries (1999) and the current model], we further assume that the population is composed of equal numbers of the two competitor types distributed across two habitats, that the good habitat has twice as many resources as the poor habitat, and that good competitors have twice the competitive ability of poor competitors.

We began by describing the outcome when competitors move between habitats simply to maximize their resource payoffs given perfect (i.e. 'ideal') information about the current payoff in each habitat. Such IFD movements will result in the familiar unequal competitors ideal free distribution (Sutherland and Parker, 1985), with the distribution of competitive units matching the distribution of resources. As noted by Parker and Sutherland (1986),

* http://www.evolutionary-ecology.com/data/1465demo.exe; or else contact either author.

there are many ways in which the two competitor types could be distributed across the habitats that will result in an IFD of unequal competitors (see 'Unequal IFD' line in Fig. 1). One of these combinations resembles an IFD of equal competitors, in that total competitor numbers, as well as total competitive units, match the distribution of resources. Interestingly, at this distribution (hereafter referred to as *M*; see Fig. 1), the distributions of

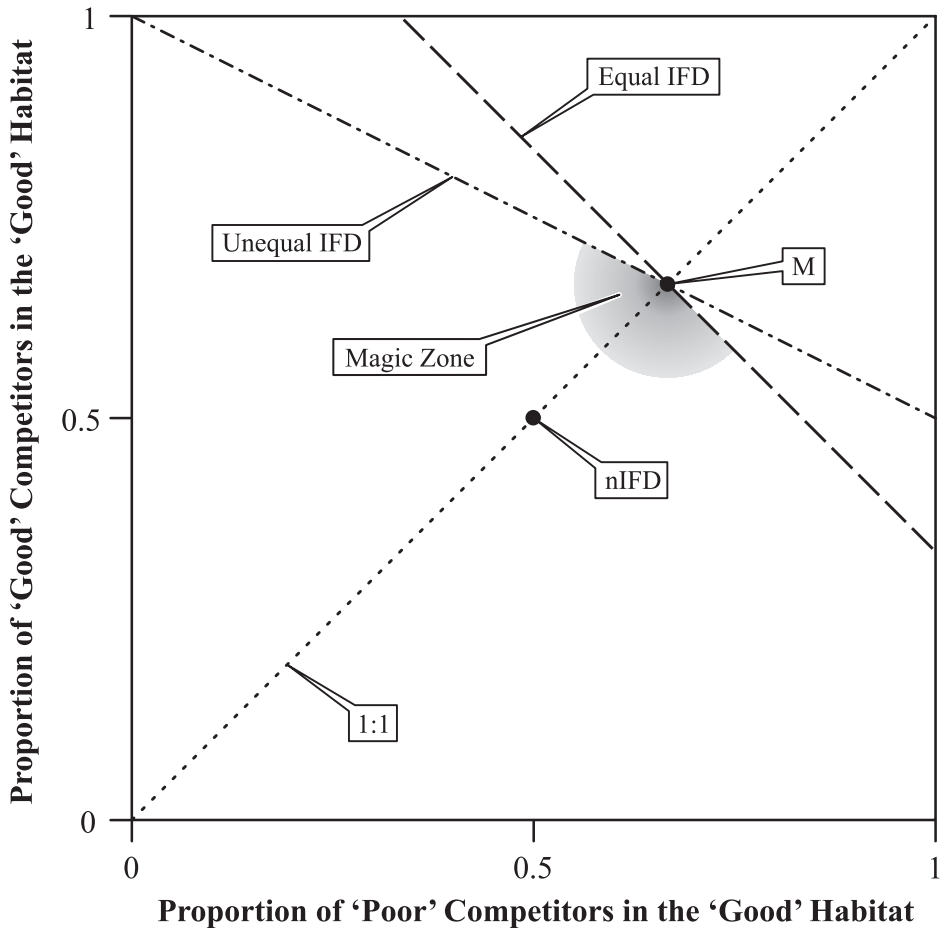

Fig. 1. A graphical representation of the predicted equilibrium distributions of two unequal competitor types distributed across two habitats, as described by Hugie and Grand (1998). When competitors move for IFD reasons alone, the predicted equilibrium distribution is not unique and can occur anywhere along the unequal competitors line (–·–·–). When they move for non-IFD reasons alone, a unique equilibrium distribution is predicted at point *nIFD*. When competitors move for IFD and non-IFD reasons combined, a unique equilibrium distribution is also predicted. Under most conditions, this 'combined' equilibrium distribution is predicted to occur in the shaded region below point *M*, the intersection of the IFD line for unequal competitors (–·–·–) and the corresponding line for equal competitors (———). Because this 'magic zone' is located close to *M*, the competitor distribution will resemble both an equal and unequal competitors IFD. However, because the magic zone is slightly below both IFD lines, the equilibrium will exhibit a slight under-matching of both competitor numbers and competitive units.

the two competitor types will be identical, with each matching the distribution of resources. Regardless, once the population reaches any one of the possible ideal free distributions, IFD movements cease, as no individual can increase its resource payoff by switching habitats.

We then described the equilibrium distribution expected when competitors move between habitats solely for non-IFD reasons. For simplicity, assume that all competitors have the same, constant probability of moving between habitats for non-IFD reasons. In this case, the distribution of competitors will be at equilibrium (hereafter referred to as *nIFD*; see Fig. 1) when there are an equal number of each competitor type in each habitat. Unlike the IFD movement equilibrium described above, *nIFD* will be a dynamic equilibrium, with non-IFD movements continuing even after the equilibrium is reached. At this equilibrium, the distributions of both competitor numbers and competitive units will be under-matched relative to the distribution of resources.

Finally, we described the equilibrium distribution expected when competitors move between habitats for both IFD and non-IFD reasons. In doing so, we demonstrated that there will no longer be a set of possible equilibrium distributions of each competitor type, as predicted by the IFD for unequal competitors (Sutherland and Parker, 1985). Instead, there will be a single, stable distribution of the two competitor types across the habitats. Not surprisingly, the predicted distribution (hereafter referred to as *C*) is a compromise between IFD movements, which equalize payoffs per competitive unit, and non-IFD movements, which equalize numbers. In most cases, distribution *C* will be characterized by under-matching of both competitor numbers and competitive units. When the relative strength of non-IFD movements is weak (as we have previously argued it will often be), the equilibrium distribution will closely resemble distribution *M*. Thus, researchers who were unaware of competitive inequalities might conclude that the distribution they observed was consistent with the predictions of the original equal competitors IFD, despite slight under-matching of total competitor numbers. Note that *C*, like *nIFD*, will be a dynamic equilibrium, with competitors moving in both directions for non-IFD reasons and from the poor habitat to the good habitat to increase their resource payoff.

MODEL

The primary goal of Hugie and Grand (1998) was to resolve a specific paradox in the IFD literature. In an attempt to generalize the problem, we did not provide specific equations, including those for describing the movements of competitors between habitats. For this reason, we begin by briefly describing a model of competitor movements for IFD and/or non-IFD reasons. We then apply this model to both large and finite population scenarios. We refer the reader to the Appendix for details about the relevant equations.

We model the distribution of two competitor types differing in their ability to compete for resources across two habitats differing in resource availability. Again, we assume that good competitors have twice the competitive ability of poor competitors and that the good habitat produces resources at twice the rate of the poor habitat. We assume that the probability of an individual undergoing an IFD movement during a given time interval will depend on the magnitude of the benefit of changing habitats (i.e. the 'switching benefit'; see equation A1). In general, the greater the relative increase in resource payoff associated with changing habitats, the greater the likelihood that an individual will undergo an IFD movement (see Fig. A1). As in Hugie and Grand (1998), we assume that competitor types will respond similarly to differences in resource payoffs between habitats. We further assume

that individuals will switch between habitats for non-IFD reasons with a constant, fixed probability, even after an IFD is reached, and that an individual's propensity to move for non-IFD reasons is independent of habitat and competitor type.

We combine these two types of movements into a single movement probability that represents the probability that an individual of a particular competitor type, in a particular habitat, will switch between habitats during a given time period (see equation A4). We apply this movement 'rule' to the large population scenario by modelling the expected proportion of each competitor type in each habitat from one time period to the next (see Appendix). In the case of the finite population scenario, we construct an individual-based model to track the movements of a finite number of individuals moving between habitats according to this 'rule' (see Appendix).

RESULTS

We begin by considering the results of the large population scenario. In doing so, we present the basic results of Hugie and Grand (1998) and also provide a test of their predictions for the specific movement model under consideration.

Large populations

Hugie and Grand (1998) assumed a large competitor population. Population size has important implications for the way in which the net movement of competitors between habitats is modelled because of the assumption that competitor movements, in particular non-IFD movements, are probabilistic events. For example, consider what will happen if individual competitors randomly switch between habitats with probability 0.5. If there are only 10 individuals in the population, the proportion of individuals changing habitats at any one time will often deviate considerably from 0.5. This might suggest that simulating the individual movements of every competitor in the population is the most appropriate way to model the net movement of competitors between habitats. We adopt this approach in a subsequent sub-section. However, the computational demands of this method increase rapidly with population size and simulation results are generally less informative than analytical solutions. Fortunately, variation due to the probabilistic nature of events at the individual level frequently decreases rapidly with increased population size and thus can be safely ignored in 'large' populations. This fact is often utilized by investigators to simplify complex phenomena by substituting deterministic models for probabilistic models. For instance, in the previous example, as population size increases, the proportion of competitors switching between habitats is less likely to deviate considerably from a value of 0.5. Thus, if a sufficiently 'large' population is assumed, the proportion of competitors switching between habitats can be assumed to be exactly 0.5. This is the approach adopted by Hugie and Grand (1998) and the large population version of the current model. In both cases, changes in the competitor distribution over time are determined by calculating the expected change in the proportion of each competitor type in each habitat given the current movement probabilities, without considering individual competitor movements (see Appendix). Although the probabilistic nature of competitor movements can be ignored completely only in an infinite population, a reasonable approximation is achieved when the population is finite but 'large'. The extent to which the conclusions of Hugie and Grand (1998) are valid for finite populations of various sizes is considered below.

Large populations: IFD movements (unequal competitors IFD)

Hugie and Grand (1998) began by considering the outcome when competitors move between habitats simply to maximize their resource payoffs given perfect (i.e. 'ideal') information about the current payoff in each habitat. As illustrated in Fig. 2a, when competitors move for IFD reasons alone, the competitor population follows a direct trajectory to the unequal competitors line. At this point, the population is at an IFD and all further movements cease, as no individual can increase its resource payoff by switching between habitats.

The particular ideal free distribution achieved depends on the initial competitor distribution, as illustrated in Fig. 2a. This result is disconcerting for two reasons. First, it suggests that, to understand animal distributions in the wild, one must know from which initial state these competitor populations were established however many hours, days or even decades ago that occurred. Second, because the resulting distribution need not resemble the equal competitors IFD, it suggests that one must always consider the complexity of competitive inequalities to predict animal distributions. We return to this point later.

Large populations: non-IFD movements (null model)

Hugie and Grand (1998) recognized that animals also move between habitats for non-IFD reasons. In the current model, we assume that all individuals switch between habitats for non-IFD reasons with the same fixed probability, regardless of habitat or competitive ability. In this case, the situation in which competitors move for non-IFD reasons alone also serves as a 'null' movement model because competitors move randomly between habitats. As expected, if individuals move randomly between habitats, they will eventually distribute themselves uniformly across those habitats. In the current case with only two habitats, each habitat will contain half the individuals of each competitor type (Fig. 2c). This equilibrium differs from the outcome when competitors move for IFD reasons alone (Fig. 2a) in two important ways. First, it is a unique equilibrium that does not depend on the initial competitor distribution. Second, it is a dynamic equilibrium; individuals will continue to move back and forth between the habitats even though the overall competitor distribution remains unchanged. This fact is not apparent from Fig. 2c. However, a close examination of the model reveals an equal proportion of each competitor type moving in opposite directions at any moment in time (see also figure 1 in Hugie and Grand, 1998).

Large populations: IFD and non-IFD movements (combined movement model)

The most important results of Hugie and Grand's (1998) model arise from their recognition that animals move between habitats for both IFD and non-IFD reasons. The results for the large population version of the current model are illustrated in Fig. 2e and support the conclusions of Hugie and Grand (1998): when animals move between habitats for both IFD and non-IFD reasons, there is no longer a set of possible equilibrium distributions as predicted by the unequal competitors model (Sutherland and Parker, 1985). Instead, there is a single, stable equilibrium distribution that does not depend on the initial distribution of competitors. Thus, competitor distributions can be explained completely using current conditions, without the need for historical data. As further predicted by Hugie and Grand (1998), when the two competitor types have the same propensity to switch between habitats

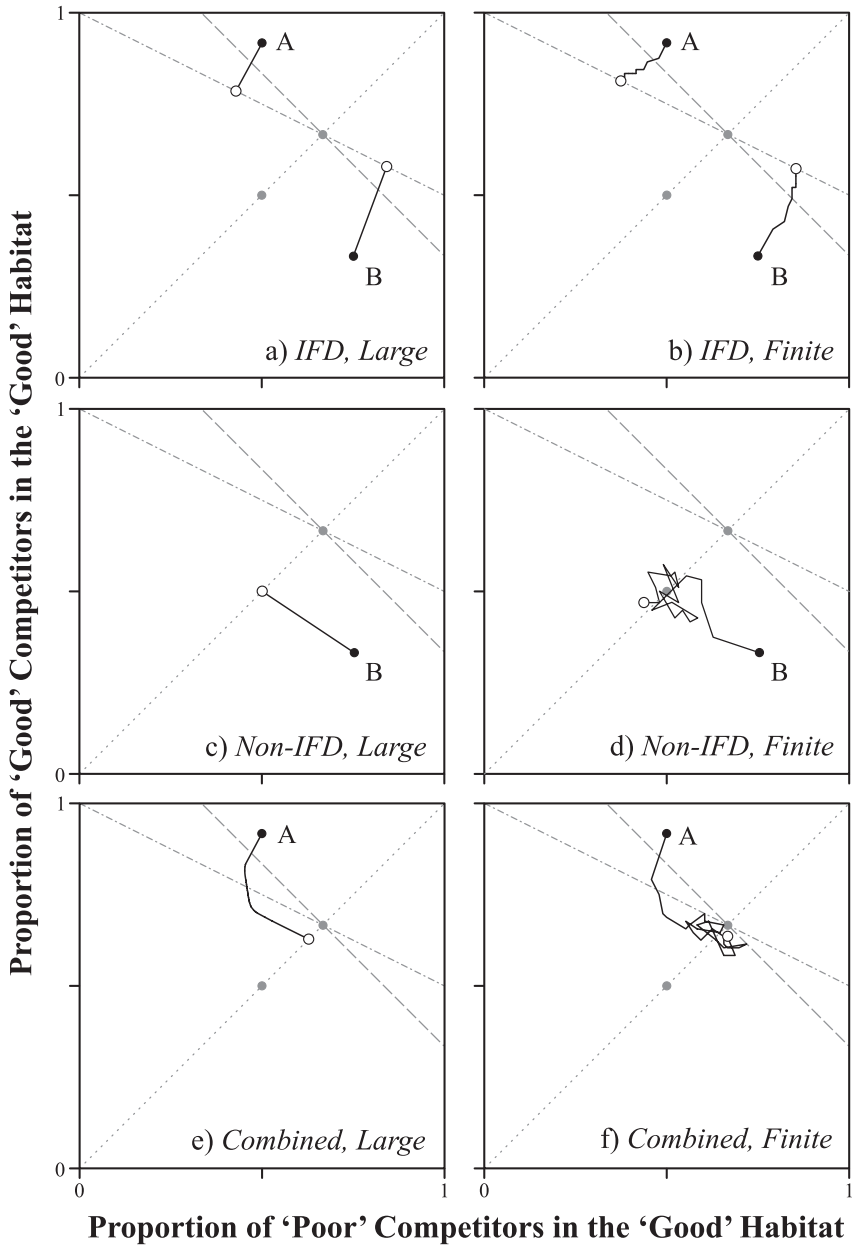

Fig. 2. The dynamics of competitor movements in large and finite populations. Each panel shows a population's trajectory from its initial distribution (•; A or B) to its distribution at the end of a simulation (○). All other lines and symbols are the same as in Fig. 1. Results are shown for both large (a, c, e) and finite (b, d, f) populations of competitors moving for IFD reasons alone (a, b), non-IFD reasons alone (c, d) and IFD and non-IFD reasons combined (e, f). In the large population scenario (a, c, e), the competitor population follows a smooth trajectory from its initial distribution to an equilibrium distribution. This trajectory does not vary between different runs of the model that start from the same initial distribution. In the finite population scenario (b, d, f), the population's

for non-IFD reasons, the equilibrium distribution falls exactly on the 1: 1 line between point *nIFD* and the unequal competitors line. Hugie and Grand argued (and the current model assumes) that the propensity of competitors to move between habitats for non-IFD reasons will be weak relative to their propensity to move for IFD reasons and, therefore, that the equilibrium distribution will be close to point *M*. This means that the distribution of competitors will resemble the equal competitors IFD in that total competitor numbers will come close to matching the distribution of resources. Again, this is exactly what is observed in the current simulation (Fig. 2e), supporting Hugie and Grand's conclusion that animal distributions can be predicted without necessarily having information about competitive inequalities. Finally, as predicted by Hugie and Grand, the observed equilibrium distribution is located in the 'magic zone' slightly below point *M* (see Fig. 1), resulting in slight under-matching of both competitive units and numbers, as is commonly observed. The results of the current simulation model indicate that Hugie and Grand (1998) did not misinterpret their results for the large population scenario they considered.

Not surprisingly, the equilibrium distribution in the combined movement model is a compromise between IFD movements, which equalize payoffs per competitive unit, and non-IFD movements, which equalize numbers. As discussed by Hugie and Grand (1998), point *C* is a dynamic equilibrium. Individuals will continue to move back and forth between habitats for non-IFD reasons. In addition, individuals will move continuously from the over-matched habitat to the under-matched habitat for IFD reasons because they can increase their resource payoff by doing so. Despite this, the net movement of competitors between habitats will be zero. This aspect of the equilibrium distribution has important consequences in finite populations.

Finite populations

Large population models remain an efficient way of modelling population processes. For example, Hugie and Grand (1998) were able to present an analytical solution to their model, including a stability analysis, and simulation of the large population version of the current model requires only a few seconds on a personal computer. However, the applicability of large (essentially infinite) population models to finite populations remains an important question. This is particularly true for models of competitor movements because experimental studies often use populations that are tiny by ecological standards. In this subsection, we explore the effect of population size on competitor distributions to determine the extent to which the results of Hugie and Grand's theory can be extended to finite populations.

We examine the effects of finite population size on competitor distribution using an individual-based modelling approach (see Appendix). This is the same approach employed by Ruxton and Humphries (1999). Both models simulate the movement of every individual

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trajectory is not smooth and varies between different runs of the model due to the probabilistic nature of individual competitor movements. Moreover, when competitors move for non-IFD reasons alone (d), or non-IFD and IFD reasons combined (f), the population never reaches an equilibrium distribution. *Note*: 96 competitors of each type were assumed for the finite model. Data for the large population model is plotted for 10,000 consecutive time periods. Data for the finite model is plotted for (b) 2000 consecutive time periods, (d) every 100th time period for 2000 time periods and (f) every 100th time period for 3000 time periods.

in the competitor population during discrete time periods. However, competitors in our model switch habitats according to the same IFD and non-IFD movement probabilities used in the large population scenario. Thus, the large and finite population versions of the current model are identical apart from the assumption of population size.

We begin by presenting the results for a finite population consisting of 96 individuals of each competitor type when competitors move for IFD reasons alone (Fig. 2b), non-IFD reasons alone (Fig. 2d), or IFD and non-IFD reasons combined (Fig. 2f). Regardless of the specific movement model used, the results of the finite population scenario differ from the large population scenario in two important ways. First, the competitor distribution now changes discontinuously, as there are a limited number of ways 96 individuals can be distributed. Second, and more importantly, the number of individuals moving between habitats is no longer completely predictable due to the probabilistic nature of competitor movements. In fact, re-running any of the simulations illustrated in Figs 2b, 2d or 2f is unlikely to yield exactly the same results. We now consider the results specific to each movement model.

Finite populations: IFD movements (unequal competitors IFD)

Figure 2b shows trajectories of a finite population of competitors moving for IFD reasons alone. The results are shown for two simulations that differ only in the initial competitor distribution. Apart from the differences already described, the overall outcome is largely unaffected by finite population size. As in the large population scenario (Fig. 2a), the population follows a trajectory (albeit now irregular) towards the unequal competitors line, at which point all further movements cease as no individual can increase its resource payoff by switching habitats. Also as before, there are many ways in which the two competitor types can be distributed between the habitats that correspond to an IFD for unequal competitors. One important difference is that the particular IFD achieved now not only depends on the initial competitor distribution, but also the particular path the population follows to the unequal competitors line.

Finite populations: non-IFD movements (null model)

The effect of finite population size is more significant when competitors move for non-IFD reasons alone. Unlike the large population scenario (Fig. 2c), the competitor population never reaches a stable distribution, but instead continues to change (Fig. 2d). This would be the case even had the simulation illustrated in Fig. 2d been initialized with an equal proportion of each competitor type in each habitat, the equilibrium in the large population scenario. This result is due, in part, to the continuous nature of non-IFD movements. At equilibrium in the large population scenario, individuals continue to move back and forth between habitats at a rate that is equal in both directions, resulting in no net change in the competitor distribution. However, in the finite population scenario, the probabilistic nature of competitor movements causes the number of individuals moving in either direction to vary. This results in variation in the net movement of competitors into a habitat and prevents any distribution from persisting indefinitely. For this reason, when competitors move for non-IFD reasons alone, the dynamic equilibrium in the large population scenario is replaced by perpetual change in the finite population scenario.

Does this result mean that our previous conclusion regarding the outcome of the null

movement model is incorrect? Should we now conclude that if competitors move randomly between habitats they will *not* be distributed uniformly across those habitats? Such a conclusion would be misleading for two reasons. First, the predicted outcome in the large population scenario is still a uniform competitor distribution. Second, it should be obvious that, while the competitor distribution is predicted to vary over time in the finite population scenario, this variation is not haphazard. As we demonstrate below, this variation is centred on the equilibrium distribution predicted under the large population scenario. Thus, even in the finite population scenario, on average competitors will remain distributed uniformly across habitats.

Finite populations: IFD and non-IFD movements (combined movement model)

The effect of finite population size on the competitor distribution when individuals move for both IFD and non-IFD reasons is similar to its effect when individuals move for non-IFD reasons alone. The competitor population never achieves a stable distribution but instead changes continuously (Fig. 2f). Again, the explanation for this result is due, in part, to the continuous nature of non-IFD movements. In the large population model, this results in a dynamic equilibrium in which individuals move back and forth continuously between habitats for IFD and/or non-IFD reasons at a rate that is equal in both directions. In the finite population scenario, however, the probabilistic nature of competitor movements causes the flow of individuals moving in either direction to vary, preventing any competitor distribution from persisting indefinitely.

Once again, this result of the finite population scenario does not affect the conclusions generated by the large population scenario. Moreover, as when competitors move for non-IFD reasons alone, variation in the competitor distribution appears to be centred on the equilibrium distribution of the large population scenario. We investigate whether this is true in the next sub-section.

Population size

Here, we ask how large a population must be before variation in the predicted competitor distribution is small enough to be unimportant. Also, we consider how accurately the equilibrium distribution in a large population model predicts the average distribution in a finite population.

We address these questions using the results of multiple simulations of the combined movement model under the finite population scenario. For comparison, we also conduct a similar analysis of the null movement model. We consider two population sizes. To provide results for a competitor population of the size representative of most laboratory studies, we selected a population consisting of 36 individuals of each competitor type (72 individuals in total). Such a population is small compared to competitor populations in the wild, which are more likely to contain hundreds or thousands of individuals. Unfortunately, simulating such large population sizes is not feasible using an individual-based approach. For this reason, we selected a more modest size of 360 individuals of each competitor type (720 individuals in total) to examine the effect of increased population size. For each population size/movement model combination, we programmed a computer to perform 10,000 simulations and summarize the results. Each simulation began with all individuals in the competitor population being randomly assigned to one of the two habitats. After

simulating 10,000 time periods, the computer recorded the distribution of competitors before beginning the next simulation. The results are summarized in Fig. 3.

As expected, variation in the competitor distribution decreases with increased population size, regardless of whether the null or combined movement model is used. Moreover, the amount of variation is comparable between the two movement models for a given population size. These observations support the view that the effect of finite population size on the combined movement model does not differ fundamentally from its effect on the null

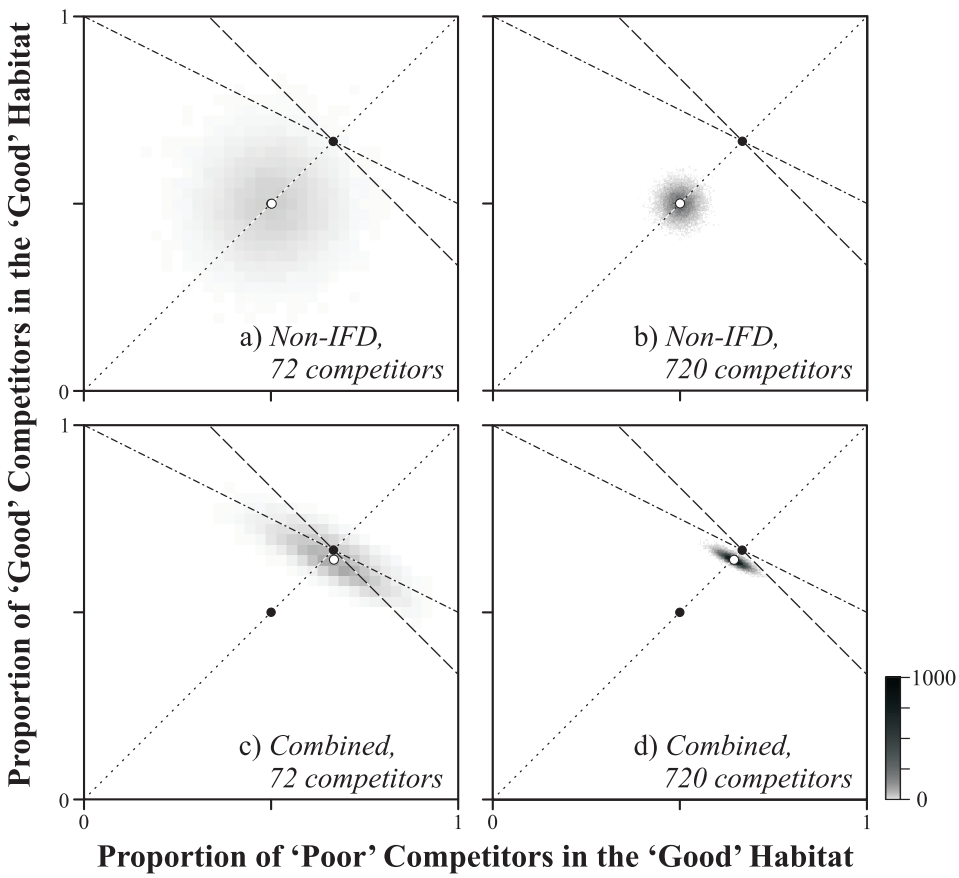

Fig. 3. The effect of population size on the probability of different competitor distributions being observed in a finite population of individuals moving for non-IFD reasons alone (a, b) and IFD and non-IFD reasons combined (c, d). Each panel shows the results of 10,000 simulations beginning with competitors randomly distributed between the two habitats. Darker areas indicate competitor distributions that were more frequently observed at the end of 10,000 time periods. Shading is scaled to approximate a continuous distribution and is, therefore, comparable between panels. The average competitor distribution after 10,000 time periods is also indicated (○). Other lines and symbols are the same as in Fig. 1. When population size is extremely small [36 individuals of each competitor type; (a, c)], the competitor distribution can vary significantly. However, as the population approaches a more ecologically relevant size [360 individuals of each competitor type; (b, c)], such variation rapidly decreases.

movement model. In both cases, conclusions based on a large population model are strictly true only for an infinitely large population, but become an increasingly good approximation as actual population size increases. For example, using large population logic, one would predict that, if competitors move randomly between habitats, they would distribute themselves evenly between those habitats. However, when the size of the competitor population is extremely small, the competitor distribution will vary considerably over time and often deviates significantly from a uniform distribution (Fig. 3a). Similarly, the distribution of an extremely small population of competitors moving for both IFD and non-IFD reasons will also vary considerably and will often lie outside the magic zone (cf. Figs 1 and 3c). In both cases, however, as the competitor population increases to a more ecologically relevant size, the competitor distribution will increasingly approximate the distribution predicted by the large population model. For example, a competitor population containing only 360 individuals of each competitor type will rarely deviate far from a uniform distribution in the null movement model (Fig. 3b) and will rarely deviate outside the magic zone in the combined movement model (cf. Figs 1 and 3d). In natural populations containing thousands of competitors, such variation should become even less relevant to the distribution of competitors across habitats.

Results from large population models can often be useful in understanding finite populations even when those populations are extremely small. Consider the prediction that when competitors move randomly between habitats, they will be distributed uniformly between those habitats. As already discussed, in small populations the competitor distribution will vary considerably over time and will often deviate significantly from a uniform distribution (Fig. 3a). However, competitors are still predicted to distribute themselves uniformly across habitats, on average. For example, the average distribution of both competitor types deviates less than 0.001 from a uniform distribution (i.e. 0.5) for the results illustrated in Fig. 3a. In the case of the combined movement model, however, the correspondence between the equilibrium distribution in the large population scenario and the average distribution in the finite population scenario is not quite exact. The average distribution of the 'good' (0.630) and 'poor' (0.656) competitors for the results illustrated in Fig. 3c deviates slightly from the corresponding equilibrium values for the large population model (0.628 in both cases). Moreover, the distributions of the two competitor types are no longer identical. There are two technical reasons for these results.

The first reason can be understood by considering that the finite population model behaves much like a large population model that experiences frequent random perturbations. In such a system, the trajectories around the equilibrium distribution become important in determining the average competitor distribution over time. In the null model, these trajectories are symmetric about the equilibrium and, therefore, the expected, average distribution in the finite model equals the equilibrium distribution in the large population model. However, because no such symmetry exists in the combined movement model, these values deviate slightly from each other.

The second reason has to do with the asymmetrical effect population size has on the switching tendencies of the two competitor types. In our model, we assume that the probability a competitor will switch between habitats for IFD reasons depends on the 'switching benefit' – the relative increase in payoff the competitor would experience if it switched habitats. More specifically, we make the simplifying assumption that, for a given switching benefit, individuals of both competitor types will move for IFD reasons with the same probability (see Appendix). In the large population model, this results in the two

competitor types having the same propensity to move for IFD reasons, as previously assumed by Hugie and Grand (1998). However, this is true only because solitary competitor movements in a large population are assumed to have a negligible impact on the resource payoffs in a habitat. When the competitor population is finite, the addition of an individual competitor to a habitat can have a significant impact on the resource payoff in that habitat. This impact is asymmetric because the payoff in a habitat is depressed more by the arrival of a good competitor than that of a poor competitor. Thus good competitors will experience smaller switching benefits and will be less likely to move for IFD reasons than will poor competitors. This asymmetry in the relative tendency of the two competitors to move for IFD reasons causes the average distribution in the finite model to deviate slightly from the 1:1 line on which the equilibrium distribution in the large population model is located.

Regardless of its causes, the deviation between the equilibrium distribution in the large population scenario and the average distribution in the finite scenario is small, even when the competitor population in the finite scenario is small by ecological standards (Fig. 3c). Moreover, this deviation decreases as population size in the finite scenario increases and becomes almost imperceptible when the population reaches a size of 720 individuals (Fig. 3d). With 720 individuals, the competitor distribution rarely deviates outside the magic zone. These observations suggest that the assumptions and conclusions of Hugie and Grand (1998) are appropriate for all but the smallest ecological populations. Moreover, even in these populations, large population models likely provide a reasonable approximation of the average behaviour of the competitor population.

A RESPONSE TO RUXTON AND HUMPHRIES (1999)

The results of the current model do not suggest any reason to believe that errors exist in either the logic or conclusions of our original model (Hugie and Grand, 1998). Moreover, our current analysis indicates that the consideration of finite population size only results in variation around the predicted equilibrium distribution as is typical of many stochastic models, including the null movement model. These conclusions are opposite to those drawn by Ruxton and Humphries (1999) based, in part, on the results of their own model of competitor movements in a finite population. To resolve these discrepancies, we examine Ruxton and Humphries' model and conclusions in some detail.

After obtaining copies of Ruxton and Humphries' original computer code, we discovered three programming errors that affect the results for their movement case (i) when Q (their movement threshold) = 0.01, and all of the results for movement cases (ii) and (iii) [see Ruxton and Humphries (1999) for further explanation of the three movement cases and the parameter Q]. However, the basic results of Ruxton and Humphries remain the same even when these errors are eliminated.

We illustrate the underlying behaviour of their model in Fig. 4a for movement case (i) and $Q = 0.01$. After moving to the unequal competitors IFD line, their competitor population moves back and forth along it, rarely departing by more than one individual from an IFD. Departures are due to non-IFD movements and are immediately followed by IFD movements that return the population to an ideal free distribution (although not necessarily the same one). This behaviour is also revealed by the variation in the competitor distribution illustrated in Fig. 4b. The darker squares along the length of the unequal competitors IFD line are IFDs. The lighter squares adjacent to this line are transitory distributions resulting from non-IFD movements.

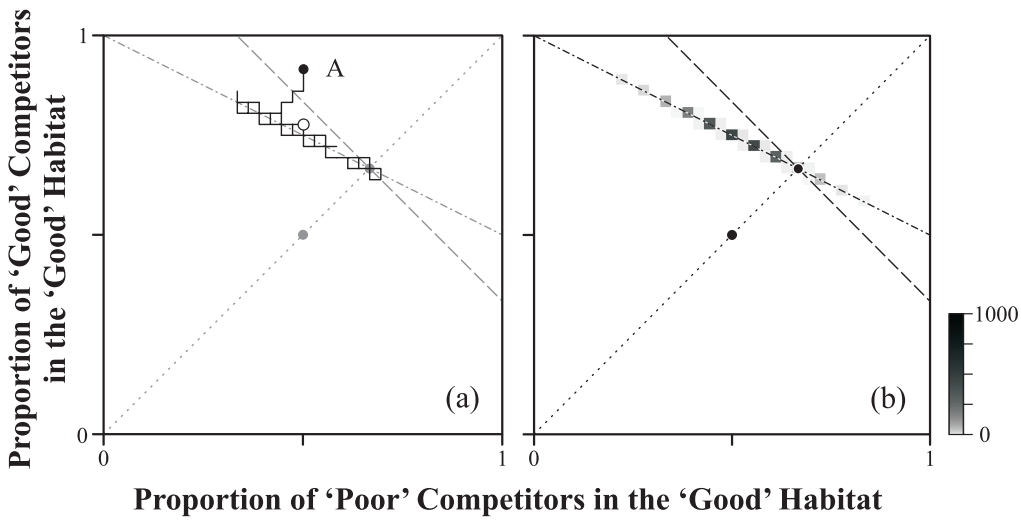

Fig. 4. The behaviour of the model presented by Ruxton and Humphries (1999) (movement rule (i), $Q = 0.01$, 36 competitors of each type). Lines and symbols are the same as in Fig. 1. Panel (a) shows a population's trajectory from its initial distribution (•; A) to its distribution at the end of a single simulation (○) lasting 20,000 time periods (10,000 'turns'). Panel (b) shows the results of 10,000 simulations beginning with competitors randomly distributed between the two habitats and lasting 20,000 time periods (10,000 'turns'). Darker areas indicate competitor distributions that were more frequently observed at the end of the simulation. Shading is scaled to approximate a continuous distribution and is, therefore, comparable to the panels in Fig. 3. As when a finite number of competitors move for both IFD and non-IFD movements in the current model (Figs 2f, 3c, 3d), the model presented by Ruxton and Humphries does not follow a smooth trajectory and never reaches an equilibrium distribution. Unlike the current model, once Ruxton and Humphries' model reaches the unequal competitors IFD line, it rarely deviates more than one individual from an IFD. This behaviour is central to the conclusions of Ruxton and Humphries.

The behaviour of Ruxton and Humphries' model is very different from the behaviour predicted by Hugie and Grand (1998). In particular, Ruxton and Humphries concluded that Hugie and Grand were incorrect in asserting that the addition of non-IFD movements to an unequal competitors IFD model will result in a single, stable equilibrium distribution. Instead, they concluded that, as when competitors move for IFD reasons alone, competitors moving for both IFD and non-IFD reasons will end up being distributed in any number of possible ideal free distributions. However, the results of Ruxton and Humphries can be explained by their underlying assumptions. These differ substantially from those of Hugie and Grand and also are unlikely to be met in nature. We return to this point below.

Hugie and Grand (1998) include an analytical proof of their assertion that, when competitors in a large population move between habitats for both IFD and non-IFD reasons, the resulting distribution is unique and asymptotically stable. Ruxton and Humphries (1999) state that this proof 'does not demonstrate anything about the number of possible equilibria; all it shows is that any possible equilibrium will be stable against infinitely small perturbations' (p. 638). They suggest that we merely identified the equilibrium properties of the unequal competitors IFD line (Fig. 2a) and mistakenly attributed them to a unique equilibrium distribution. However, an equilibrium point is asymptotically stable if, and only

if, the system returns to it after a small perturbation in *any* direction (Glendinning, 1994; Beltrami, 1998). This is *not* the case for the points along the unequal competitors IFD line because the population will remain at equilibrium if a perturbation moves it along the length of this line. Nothing will cause such a system to return to its original equilibrium point because a change from one ideal free distribution to another is irrelevant to the competitor population. In contrast, our proof of the asymptotic stability of point *C*, the combined equilibrium, in our earlier model ensures that it is a *single*, stable distribution. This conclusion is supported by the results of the large population model in the current paper (Fig. 2e). Ruxton and Humphries offer no additional evidence that our original model contains errors or is based on unrealistic assumptions about competitor movements.

Although Ruxton and Humphries (1999) offer no compelling reason to doubt the results of Hugie and Grand (1998), their model does potentially provide an alternative way of modelling competitor movements. However, we will now argue that the behaviour of Ruxton and Humphries' model results from unrealistic assumptions that effectively eliminate the influence of non-IFD movements on the competitor distribution. The explanation for why this is the case is best understood in the context of the equal competitors model.

Consider how a group of 36 equal competitors should distribute themselves between two habitats, one with twice the resource availability of the other. If competitors only moved for IFD reasons, one would expect 24 of them to occur in the good habitat. Similarly, if competitors moved randomly between habitats for non-IFD reasons alone, one would expect them to be evenly distributed, with 18 individuals occurring in each habitat. Now consider what happens if competitors move for both IFD and non-IFD reasons. The expected competitor distribution will depend on the relative propensities of competitors to move for IFD and non-IFD reasons. In particular, the more likely competitors are to move for non-IFD reasons, the more evenly one would expect them to be distributed between the two habitats. This is exactly what occurs in our models of competitor movements (see Hugie and Grand, 1998, and Fig. 5a). In contrast, the competitor distribution produced by Ruxton and Humphries' model *never* deviates more than one individual from an IFD distribution, even when the propensity of competitors to move for non-IFD reasons is at its maximum value (Fig. 5b). The same results would be obtained even if the population contained millions of individuals. This example demonstrates the constant, overwhelming influence of IFD movements in Ruxton and Humphries' model.

One might argue that Ruxton and Humphries' model merely presents an alternate view of the relative importance of IFD and non-IFD movements; specifically, that IFD movements will immediately correct any deviation from an ideal free distribution due to a single non-IFD movement. To accept this viewpoint, however, one must accept the assumptions on which it rests. We now compare the assumptions of our respective approaches. There are fundamental differences between them.

Although IFD theory is concerned with the distribution of animals over space (Fretwell and Lucas, 1970; Fretwell, 1972), evaluating the dynamics of competitor movements necessarily requires consideration of time. Our models explicitly consider time: either continuously (in the case of Hugie and Grand, 1998) or in discrete time periods (in the current model). In contrast, competitors in Ruxton and Humphries' (1999) model move during successive 'turns'. Each turn actually consists of two discrete time periods: one in which a non-IFD movement may occur, followed by another, in which an IFD movement may occur. This alternating between non-IFD and IFD movements during successive time periods assumes that animals are unable to make decisions simultaneously about non-IFD

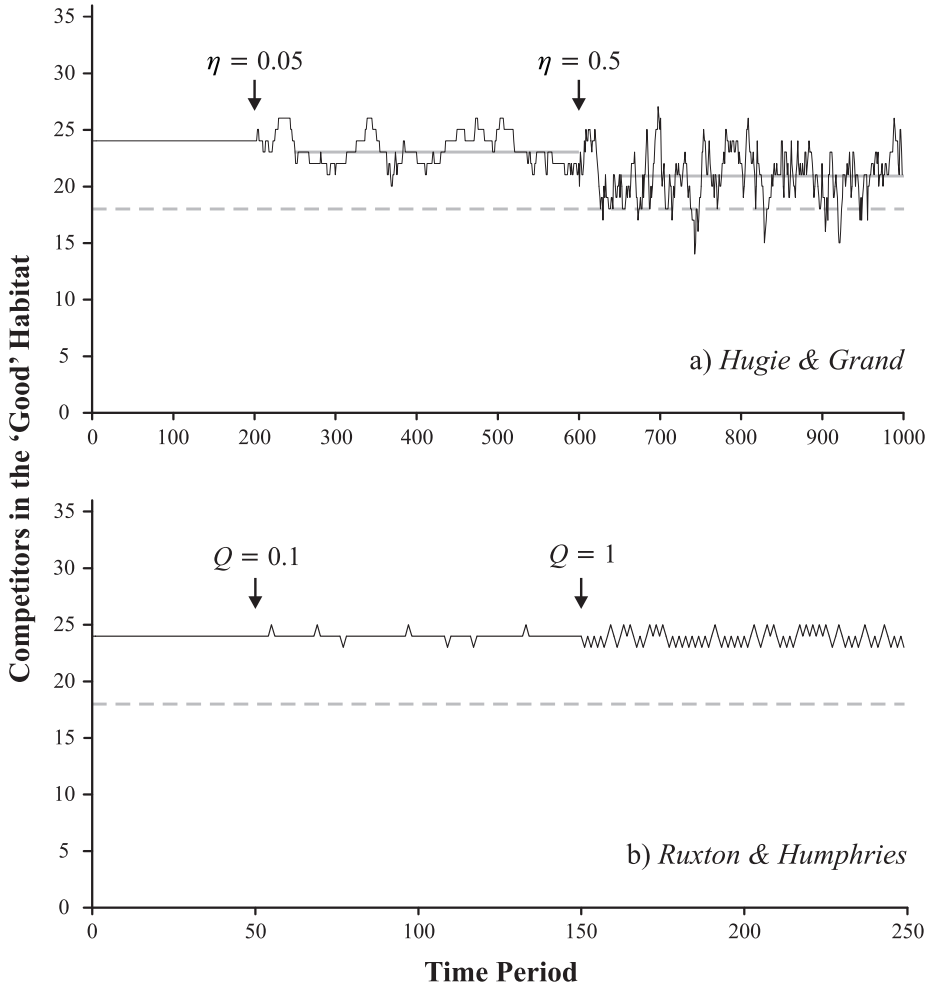

Fig. 5. The effect of the non-IFD movement probability (η or Q) on the distribution of a finite number of equal competitors (36) distributed between two habitats as modelled (a) in the current combined movement model and (b) by Ruxton and Humphries (1999) [movement rule (i)]. In both cases, the non-IFD movement probability was initially zero and was increased twice during the simulation. The solid black line indicates the actual competitor distribution during each time period. The solid grey line shows the average competitor distribution during the indicated time periods and the dashed line shows the expected competitor distribution if individuals moved for non-IFD reasons alone (an equal number in both habitats). When non-IFD movements do not occur, competitors in both models follow an ideal free distribution (24 of 36 competitors in the good habitat). When the non-IFD movement probability (η or Q) is increased, random competitor movements between habitats increase in both models. In the current model (a), this results in a competitor distribution that is increasingly variable over time and more evenly distributed between the two habitats, on average. In contrast, random movements in Ruxton and Humphries' model never result in a competitor distribution that deviates more than one individual from an ideal free distribution, even when non-IFD movements occur with the maximal probability ($Q = 1$). This result would be obtained even if the population contained millions of individuals. Note that while η and Q are not strictly comparable, both intend to model non-IFD movements as described in Hugie and Grand (1998).

and IFD movements. It also assumes that animals alternate between considering non-IFD and IFD movement decisions in strict synchrony across the entire population. In comparison, individual competitors in our models simultaneously consider their non-IFD and IFD options and are free to move between habitats for either reason at any time.

Ruxton and Humphries' (1999) model restricts the number of competitors that can move between habitats during a given time period to a single individual. This assumes that competitor movements are not independent of one another. In the case of non-IFD movements, the individual that moves is selected at random. In the case of IFD movements, the individual that moves is the one that would benefit the most from switching habitats. All other competitors refrain from moving during that time period, even if they would benefit from doing so. In our models, individuals move independently of one another, as one would expect if animals were concerned solely with their own fitness.

Finally, in Ruxton and Humphries' model, exactly one IFD movement occurs during every second time period regardless of whether changing habitats increases a competitor's resource payoff by 0.001% or by 1000%. In contrast, IFD movements in our current model are probabilistic and occur at rates that increase with the benefit of changing habitats.

The assumptions of Ruxton and Humphries (1999) explain the results illustrated in Fig. 5b. Deviations from an ideal free distribution are limited to a solitary individual because only one individual is allowed to undergo a non-IFD movement during an eligible time period. Moreover, because an IFD opportunity always follows in the next time period, any such deviation is always immediately corrected. Figure 5b also demonstrates an important difference between our coefficient η and Ruxton and Humphries' coefficient Q. Although both probabilities control the level of non-IFD movements in the population, they are not equivalent. Our coefficient η is the probability that an individual competitor will move between habitats for non-IFD reasons during any given time period. Ruxton and Humphries' Q is the probability that one, and *only* one, individual will undergo a non-IFD movement during every *second* time period.

In constructing our models, we assumed that an individual competitor will make the decision to move between habitats by simultaneously considering its foraging and non-foraging options and choosing a course of action based on the consequences to its own fitness. This assumption is reasonable given our understanding of how animals make decisions (see Lima and Dill, 1990, for a review). To accept Ruxton and Humphries' (1999) argument, one must accept that competitors make movement decisions by alternatively considering foraging and non-foraging decisions in strict synchrony across the entire population. One must also accept that more than one competitor will never decide to undergo a non-IFD movement at the same time, even in a population containing thousands of individuals. Finally, one must accept that, following any non-IFD movement in a population, all further non-IFD movements are inhibited until an opportunity for an IFD movement occurs. We believe these assumptions to be unrealistic and hence question the usefulness of Ruxton and Humphries' model. At best, Ruxton and Humphries (1999) demonstrate only that the conclusions of Hugie and Grand (1998) do not apply under the former's very specific and novel competitor dynamic.

CONCLUSIONS

The results of the current model do not suggest any reason to believe that errors exist in either the logic or conclusions of Hugie and Grand (1998). In fact, when the large

population assumption of Hugie and Grand is met in the current model, the results match exactly their predictions. Moreover, our analysis indicates that finite population size only results in variation around the predicted equilibrium distribution, as is typical of many stochastic models. At ecologically relevant population sizes, this variation was found to be small enough to justify the large population assumption of Hugie and Grand (1998). Even in small populations, the large population model reasonably predicted the average distribution of competitors in the population. For these reasons, we conclude that the theory presented by Hugie and Grand is quite general and that non-IFD movements likely play an important role in determining the ecological distribution of competitors. In particular, non-IFD movements remain an important explanation for why animal distributions often approximate an equal competitors IFD despite the existence of competitive inequalities among individuals.

ACKNOWLEDGEMENTS

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APPENDIX: A GENERAL MODEL OF COMPETITOR MOVEMENTS BETWEEN HABITATS

In this appendix, subscripts refer to competitor types and superscripts to habitats. The symbol $i \rightarrow j$ refers to a competitor movement from habitat i to habitat j.

IFD movements

An IFD movement is said to have occurred whenever a competitor that has perfect (i.e. 'ideal') information about the current resource payoff in each habitat switches 'freely' (i.e. without interference) from one habitat to another to improve its resource payoff. To model such movements, let $s_k^{i \rightarrow j}$

be the 'switching benefit' – the relative increase in resource payoff a competitor of type k would receive if it switched to habitat j from its current habitat i. We calculate $s_k^{i\to j}$ in relative terms so that its value does not depend on the units used to measure resource payoffs. The details of these calculations are presented below [see equations (A7) and (A9) for the switching benefit in the large and finite population model, respectively].

Whenever $s_k^{i\to j}$ is positive, an individual of competitor type k should move from habitat i to habitat j for IFD reasons. We assume that a competitor will switch habitats for IFD reasons during a given time period with some probability that increases as the benefit of such a move increases. Let $\gamma_k^{i\to j}$ be the probability that a competitor of type k will move from habitat i to habitat j for IFD reasons alone during a given time period:

$$\gamma_k^{i\to j}=\begin{cases}0 & \text{if } s_k^{i\to j}\le 0\\ \dfrac{(s_k^{i\to j})^{\alpha_k^{i\to j}}}{(s_k^{i\to j})^{\alpha_k^{i\to j}}+(\beta_k^{i\to j})^{\alpha_k^{i\to j}}} & \text{if } s_k^{i\to j}>0\end{cases} \tag{A1}$$

where $\alpha_k^{i\to j}>1$ and $\beta_k^{i\to j}>0$. The value of $\gamma_k^{i\to j}$ is a function of the switching benefit $s_k^{i\to j}$, as illustrated in Fig. A1. When the benefit of switching is small, the probability of a competitor moving for IFD reasons is low. As the switching benefit increases, this probability also increases, slowly at first, then more rapidly as the fitness benefits of acquiring more resources dramatically increase. Eventually, the increase in the probability of a competitor undergoing an IFD movement begins to decelerate as

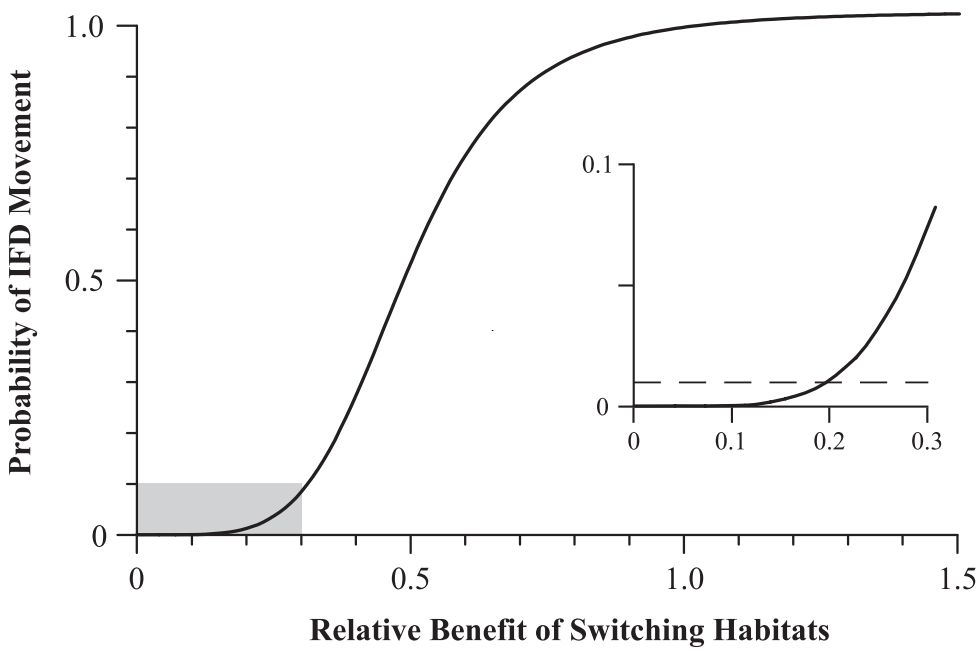

Fig. A1. Probability that an individual of type k will switch from its current habitat i to a habitat j for IFD reasons alone ($\gamma_k^{i\to j}$) as a function of the 'switching benefit' ($s_k^{i\to j}$) – the relative increase in resource payoff the competitor would receive if it switched habitats. The shaded region is shown in more detail in the inset graph. The dashed line indicates a value of 0.01, the value assumed for the probability that an individual will switch habitats for non-IFD reasons (η).

additional resources yield smaller increases in fitness due to limitations in the amount of resource a competitor can utilize. The exact shape of the function illustrated in Fig. A1 is determined by the coefficients $\alpha_k^{i\to j}$ and $\beta_k^{i\to j}$ in equation (A1). The coefficient $\beta_k^{i\to j}$ is the value of $s_k^{i\to j}$ for which $\gamma_k^{i\to j} = 0.5$, and $\alpha_k^{i\to j}$ determines how rapidly $\gamma_k^{i\to j}$ increases at this point.

In most cases, there will be little reason to assume that a competitor's propensity to move for IFD reasons will vary across habitats. For this reason, equation (A1) can usually be simplified by replacing $\beta_k^{i\to j}$ and $s_k^{i\to j}$ with the terms β_k and α_k, respectively. Furthermore, if one also assumes that the propensity for IFD movements does not vary between competitor types (as in Hugie and Grand, 1998), equation (A1) can be simplified further by replacing β_k and α_k with the terms β and α, respectively. To allow direct comparison between our current and previous models, we continue with these assumptions. We choose the coefficient values $\alpha = 5$ and $\beta = 0.5$. At these values, the probability of a competitor switching habitats for IFD reasons alone increases sharply once the switching benefit reaches 15%, but rapidly asymptotes once it exceeds 60% (see Fig. A1).

Non-IFD movements

We define a fixed probability $\eta_k^{i\to j}$ that a competitor of type k will move from habitat i to habitat j for non-IFD reasons alone during a given time period. If a competitor's propensity to move for non-IFD reasons does not vary across habitats (see Hugie and Grand, 1998), the model can be simplified by replacing $\eta_k^{i\to j}$ with the term η_k. Furthermore, if the propensity for non-IFD movements does not vary between competitor types, the model can be simplified further by replacing η_k with the term η. We make both of these simplifying assumptions in the current model. We assume a value of $\eta = 0.01$. Thus, we assume that non-IFD movements are rare relative to IFD movements (compare η with $s_k^{i\to j}$ in Fig. A1).

Movement probabilities

Let $\phi_k^{i\to j}$ be the probability that a competitor of type k will move from habitat i to habitat j during a given time period. The calculation of $\phi_k^{i\to j}$ will depend on whether competitors move

- for IFD reasons alone:

$$\phi_k^{i\to j} = \gamma_k^{i\to j} \tag{A2}$$

- for non-IFD reasons alone:

$$\phi_k^{i\to j} = \eta_k^{i\to j} \tag{A3}$$

- for IFD and non-IFD reasons combined:

$$\phi_k^{i\to j} = \gamma_k^{i\to j} + (1 - \gamma_k^{i\to j})\,\eta_k^{i\to j} \tag{A4}$$

Computer simulation requires that we model competitor movements during discrete time intervals. Discrete intervals can cause instability in dynamical models because of the inherent time lags that they introduce. This problem manifests itself in the current model when the probability that a competitor will switch habitats during a given time period becomes too large. For example, a large proportion of the population may move from one habitat to another for IFD reasons, only to find the payoff in the new habitat sufficiently depressed to cause them all to return to their original habitat in the very next time period. Such oscillations can continue indefinitely.

One solution is to model time more continuously by assuming smaller time intervals. We achieved virtually the same effect by reducing the magnitude of the movement probabilities. (The smaller the

time intervals, the less likely a competitor will switch habitats during a given interval.) We introduce a scaling coefficient λ (where $0 \leq \lambda < 1$) to produce a new, scaled probability that a competitor of type k will move from habitat i to habitat j during a given time period:

$$\theta_k^{i \to j} = (1 - \lambda)\, \phi_k^{i \to j} \tag{A5}$$

Damping of potential oscillation occurs when $\lambda > 0$. We used a value of $\lambda = 0.9$ in all runs of the model.

Large population model

Applying the above movement model to a large population involves modelling the expected proportion of each competitor type in each habitat from one time period to the next. Because we consider only two habitats, the distribution of type k competitors in the current time period is completely specified by p_k^1, the proportion of those competitors in habitat 1. The distribution of type k competitors in the next time period will be:

$$\tilde{p}_k^1 = p_k^1 + (1 - p_k^1)\, \theta_k^{2 \to 1} - p_k^1 \theta_k^{1 \to 2} \tag{A6}$$

Iterating equation (A6) for both competitor types yields subsequent distributions.

Since the population is large, the addition of a single competitor to a habitat is assumed to have a negligible effect on the resource payoffs in that habitat. Thus, the switching benefit is given by:

$$s_k^{i \to j} = \frac{r^j - r^i}{r^i} \tag{A7}$$

where r^i is the current resource payoffs in habitat i. This value is calculated as follows:

$$r^i = \frac{R^i}{p_1^i N_1 K_1 + p_2^i N_2 K_2} \tag{A8}$$

where R^i is the available resources in habitat i, K_k is the competitive weight of type k competitors and N_k is the total number of type k competitors in the population. In the large population scenario, the switching benefit is the same for both competitor types, so the term $s_k^{i \to j}$ can be replaced with $s^{i \to j}$ in all equations. Also note that while r^i is calculated as a payoff per competitive weight, the same value of $s_k^{i \to j}$ is obtained whether resource payoffs are calculated in this way or in absolute terms.

Finite population model

Applying the movement model to a finite population involves simulating the individual movements of competitors between habitats. During each time period, each competitor switches habitat with probability $\theta_k^{i \to j}$. In this scenario, the switching benefit, $s_k^{i \to j}$, is given by:

$$s_k^{i \to j} = \frac{r_k^{i \to j} - r^i}{r^i} \tag{A9}$$

where r^i is the current resource payoff in habitat i and $r_k^{i \to j}$ is the resource payoff a competitor would receive if it switched to habitat j. Here, the movement of one member of a finite population to a new habitat is assumed to have a significant impact on the resource payoff in that habitat. Adding that one individual to the denominator of $r_k^{i \to j}$, we obtain:

$$r^i = \frac{R^i}{n_1^i K_1 + n_2^i K_2} \tag{A10}$$

$$r_k^{i \to j} = \frac{R^j}{K_k + n_1^j K_1 + n_2^j K_2} \tag{A11}$$

where n_k^i is the number of competitors of type k currently in habitat i. As before, $r_k^{i \to j}$ and r^i are calculated as payoffs per competitive weight, but the same value of $s_k^{i \to j}$ is obtained whether resource payoffs are calculated in this way or in absolute terms.